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TABLE 1
PLANT FORMATIONS IN THE SIERRA DE TUXTLA

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- (2) Montane Rain Forest or Cloud Forest (*Englehardtia-Quercus* Association)
- (3) *Liquidambar-Quercus* Associes
- (4) Montane Thicket (*Podacarpus-Thouinidium* Association)
- (5) Elfin Woodland (*Quercus-Clusia-Podacarpus* Association)

B. SEASONAL FORMATIONS
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- (7) *Bursera-Sabal-Orbignya* Associes

C. SEASONAL-SWAMP FORMATIONS
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E. SWAMP FORMATIONS
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- (13) Mangrove Woodland (*Rhizophora* Consociation)

F. MISCELLANEOUS FORMATIONS
- (14) Recently Abandoned Milpas
- (15) Pastures
- (16) Hedgerows

FIGURE 2
Vegetation of the Sierra de Tuxtla.

The analyses of the vegetation in the following discussion are based on samplings by both Andrle and myself. In no instance was an effort made to completely characterize a vegetative type. Usually only the apparently more common members that were either in blossom or fruit were collected. (All plant specimens were donated to the United States National Museum.) Throughout the discussion plant species are listed in descending frequency of abundance. Also, several terms belonging to the science of plant ecology are used, and in order to avoid confusion, are defined below.

1. Dominant—"those members of the community which exert a controlling influence over the other components" (Beard, 1944). These were chosen empirically according to size and abundance.

2. Association—"the largest possible group which has consistent dominants" (Beard, 1944). When possible I have tried to characterize the association with the generic names of the two most common dominants. However, in certain instances this limitation could not be imposed so three names had to be employed.

3. Consociation—"a group of equivalent rank to the association where there is only one clear dominant" (Beard, 1944).

4. Associes—the major unit of a sere (Clements, 1936), a sere being defined as "any community which is patently in a state of change, development or transition" (Beard, 1944).

MONTANE FORMATIONS

Although Andrle (1964) classified all of the relatively undisturbed and "tall forests" of the range in two categories—"Rain Forest" and "Cloud Forest"—he did recognize that the formations were not homogeneous throughout their extent. My investigations indicate that the diversification within each type is sufficiently pronounced to warrant the formations divisions into subcategories, which can be correlated with the various "Montane Formations" of Beard (1955).

1. Lower Montane Rain Forest (*Terminalia-Dalbergia* Association); Plate 5.

This formation encompasses the "Rain Forest" of Andrle (1964) and exists principally on the slopes of the major volcanoes. On the Gulf slopes the formation occurs within an altitudinal range of approximately 50 to 3,000 feet. The most extensive areas remaining south of the high long axis of the range

PLATE 5
Lower Montane Rain Forest near Vigía. May 1965, 1,700 feet.

are in the vicinity of Cerro Cintepec, the Curbres de Bastonal, and southwest of Volcán San Martín Tuxtla (Andrle, 1964).

Until five to seven years ago the forest on the Gulf slopes was relatively undisturbed by man. But since then there has been a rather steadily accelerating movement of people from the more densely populated leeward slopes around and onto the Gulf facing slopes. This in turn has resulted in forest destruction so that presently there exist rather extensive (but disjunct) areas that are already cleared or are in the process of being cleared. On the leeward slopes the forest is very much reduced because of several factors. First, because of extensive cultivation involving both corn and coffee, the former ccurring in no restricted zone and the latter occurring principally in a zone between 2,300 and 2,900 feet in elevation; second, because of a relatively low annual precipitation due to a rain shadow effect; and third, because of unfavorable edaphic conditions, particularly on the Santa Marta massif.

Andrle (1964) stated that the "Rain Forest" seems to have its nearest affinities with the "Seasonal Evergreen Forest" of Beard (1944) because of the presence of an understory composed principally of palms and because several of the dominant trees exhibit buttressing. However, as indicated subsequently by Beard (1949), these two characteristics are also shared by the Lower Montane formation but that the critical factors that determine the Lower Montane formation are the presence of only two distinct tree strata and simple leaved dominants, both of which are characteristic of the forests at relatively low elevations in the Sierra. Furthermore, since the three formations that exist on the slopes at higher elevations correlate very well with other subdivisions in Beard's Montane sequence, I conclude that the forests between 50 and 3,000 feet should be considered a typical Lower Montane Rain Forest.

The flora within this formation is very rich. Ground vegetation is relatively sparse and includes *Aphelandra aurantiaca* and *Didymochlaena truncatula* (Andrle, 1964). Above this is a zone of saplings and shrubs, which include *Hamelia longipes, Myriocarpa longipes, Cephaelis elata* (Andrle, 1964), *Psychotria* sp., and *Deherainia smaragdina.* Because of the relative sparseness of ground vegetation, walking upright in the formation is not difficult.

The lowest tree stratum ranges between 10 and 18 feet and is composed predominantly of palms—*Astrocaryum mexicanum*

PLATE 6
Montane Rain Forest or Cloud Forest on Volcán Santa Marta. April 1965, 3,200 feet.

and *Chamaedarea tepejilote* being the most common. The dicot *Aegiphila costaricensis* is also very common.

A distinct middle stratum cannot be differentiated from an upper stratum of emergents. In most cases the tallest trees—*Terminalia amazonia, Dalbergia* sp. and *Bernoullia flammea, Talauma mexicana, Pithecollobium arboreum, Mirandaceltis monoica, Phoebe mexicana, Engelhardtia guatemalensis,* and *Virola guatemalensis* (Andrle, 1964)—although ranging from 90 to 110 feet in height, do not protrude significantly above the canopy to warrant the title of emergents. Thus it is best to combine them with the slightly lower species such as *Pseudolmedia oxyphyllaria, Stemmadenia galeottiana, Pleuranthodendron mexicana, Calatola* sp., *Cletha macrophylla, Saurauia* sp., *Annona* sp., *Coccolaba* sp. (Andrle, 1964), and *Rinorea guatemalensis* into a single upper stratum or canopy layer that ranges between 70 and 110 feet in height.

Lianas and the climbing fern *Dryopteris* sp. are common on the trunks of many trees. Epiphytes are relatively uncommon and occur principally in tree crowns.

Within this formation there appears to be a continual shedding of leaves by the component species although there is a heavier leaf fall near the end of the dry season (May). Only *Bernoullia flammea* was observed to lack leaves for any extended period during the dry season. Also, there appears to be no distinct flowering or fruiting season although flowering, like leaf fall, is more common towards the end of spring.

Where relatively substantial openings exist in the forest, e.g., along logging roads and trails, *Boeheria* sp. and *Urera elata* usually form dense thickets, which attain maximum heights of 8 to 12 feet.

2. Montane Rain Forest or Cloud Forest (*Englehardtia-Quercus* Association); Plate 6.

This formation is located above the Lower Montane formation and ranges between approximately 3,000 and 4,100 feet on Volcáns San Martín Tuxtla and Santa Marta but to only 3,500 feet on Volcán San Martín Pajapan because of the latter's slightly lower elevation.

Ground vegetation is similar to that in the Lower Montane formation. Above the ground cover is a zone of saplings and shrubs of which the most common are *Cephaelis elata, Chamaedorea ernesti-augustii, Deppea excelsa, Rudgea cornifolia, Engelhardtia mexicana,* and *Ceratozamia mexicana.*

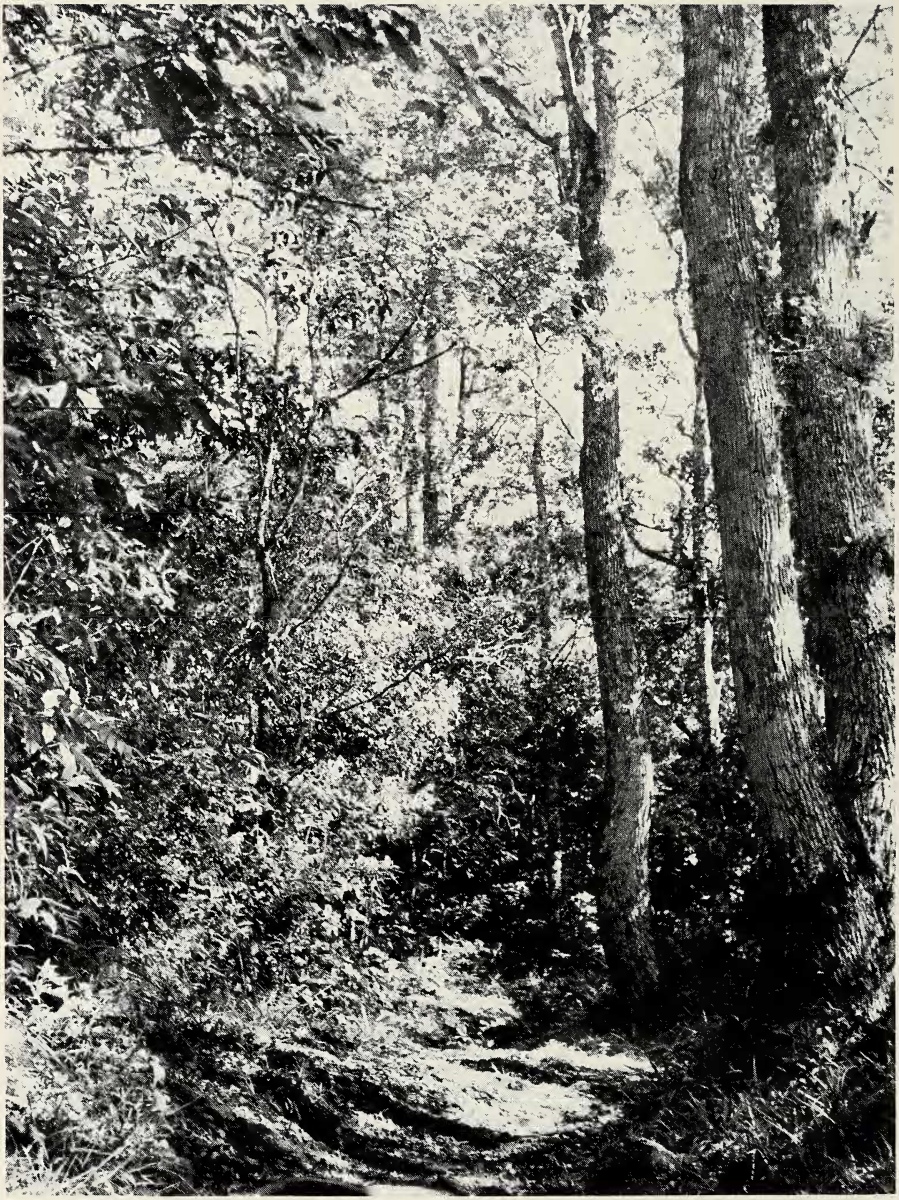

PLATE 7
Gum-oak forest on Volcán Santa Marta. May 1965, 2,700 feet.

Only two tree strata are present. The lower stratum ranges between 15 and 30 feet and includes *Eugenia* sp., *Chamaedorea elegans, Chamaedorea* sp., *Eupatorium tuerckheimii, Solanum schlechtendalianum,* and *Carpinus caroliniana.* Tree ferns, *Cyathea* sp. and *Alsophila schiedeana* (Andrle, 1964), are very common in the numerous ravines and ridge slopes.

The upper stratum ranges between 50 and 70 feet and includes *Engelhardtia mexicana, Quercus skinneri,* and *Rheedia edulus.*

Lianas and epiphytes are more common than in the Lower Montane formation; epiphytes are not restricted to tree boles. Trunks and limbs usually are festooned with mosses, algae, and ferns.

3. *Liquidambar-Quercus* Associes; Plate 7.

The gum-oak forest, which appears to be a subclimax community, is restricted to a narrow zone on the southern slopes of Valcán Santa Marta between elevations of 2,500 and 3,000 feet. However, both dominants occur sporadically in the Montane Rain Forest on Volcán San Martín Tuxtla and on small isolated hill slopes northeast and northwest of Lago Catemaco.

Ground vegetation is relatively sparse although there is a dense understory of shrubs, bushes, and saplings of which the most common are *Cephaelis elata, Siparuna andina, Phoebe bourgeauviana, Erythroxylon tabascense, Hirtella racemosa, Rinorea guatemalensis, Croton glabellus, Rondelitia galeottii, Persea longipes, Machaonia* sp., and *Casearia sylvestris.*

The understory forms a gradient up to the canopy layer that ranges between 30 and 50 feet in height and which consists primarily of *Liquidambar styraciflua, Quercus ghiesbrechtii, Belotia* sp., *Casearia nitida,* and *Alchornea latifolia.*

The gum trees usually drop their leaves in early February and remain leafless for approximately two to three weeks after which time new growth and blossoms appear. The oaks usually do not lose their leaves until late March or early April; new growth and blossoms appear immediately thereafter.

Andrle (1964) suggests that the gum-oak forest exists because of a combination of factors—destruction of the preexisting vegetation by man, lowered soil fertility from extensive weathering, and rainfall that is slightly lower than that in other sections of the Sierra because of the "broad, high front presented by the south crater walls of Cerro Campanario and Volcán Santa Marta."

PLATE 8
Montane Thicket on Volcán Santa Marta. April 1965, 4,700 feet.

Although all three factors probably are operational, it is my opinion that the first two are of greater significance than the third. The Popoluca Indians have been intensively utilizing the area within the present-day gum-oak forest for the cultivation of their corn and coffee for hundreds of years since corn and coffee do not grow well in the pine and oak forests that surround the Indian villages. The corn fields are used only for three to five consecutive years; they then are abandoned and succession is allowed to proceed. Within 20 to 30 years a rather substantial forest of gum and oak becomes established. This is then cut and burned and hence the cycle is begun anew. Very few areas are allowed to proceed beyond the gum-oak community for arable land is at a premium. However, those few areas that remain uncut for longer periods develop a forest that gradually acquires the characteristics of the Montane Rain Forest that occurs presently slightly higher in elevation. Thus, I conclude that intensive agriculture with its inevitable lowering of soil fertility is the primary factor for the existence and maintenance of the *Liquidambar-Quercus* Associes in the Sierra and that this associes is a subclimax community in the Montane Rain Forest formation.

4. Montane Thicket (*Podacarpus-Thouinidium* Association); Plate 8.

This formation, which corresponds in part to the "Cloud Forest" of Andrle (1964), occurs between approximately 4,100 and 4,800 feet on Volcáns San Martín Tuxtla and Santa Marta but is absent on Volcán San Martín Pajapan. In physiognomy the forest is slightly modified from that described by Beard (1949) inasmuch as there is a distinct and dense understory of shrubs and small trees in addition to the canopy layer. This understory ranges between approximately 15 and 30 feet in height and consists principally of *Clethra suaveolens, Oreopanax xalapense, Oreopanax capitatum, Xylosma* sp. (Andrle, 1964), *Engelhardtia mexicana, Ardisia* sp. (?), *Thouinidium decandrum, Eugenia* sp., *Deppea excelsa,* and *Rudgea cornifolia.*

The canopy layer ranges between 45 and 60 feet in height and is composed principally of *Podocarpus oleifolius, Thouinidium decandrum,* and *Engelhardtia mexicana.*

Tree trunks (usually with no extensive buttressing) and branches support luxuriant growths of mosses, lycopodiums, ferns, bromeliads, and orchids (*Elleanthus capitatus* being a common species). Lianas aren't as common as in the Montane

PLATE 9
Elfin Woodland on peak of Volcán Santa Marta. April, 1965, 5,100 feet.

Rain Forest.

The forest on the crests of several of the steep ridges on Volcán Santa Marta has been cut by the Popoluca Indians in order to establish hunting trails up to the crater. In these relatively open areas there is a seral community in which the palms *Chamaedorea elegans, Chamaedorea ernesti-augustii,* and *Chamaedorea* sp. predominate and which tends to resemble the "Palm Break" subclimax community of Beard (1944; 1949). However, because of the restricted distribution of this community in the Sierra, I think that the community does not warrant the rank of formation.

This formation (and the succeeding one) frequently are enveloped in clouds caused by the condensation of moist air moving in on the north and northeast winds from the Gulf. Although mist is more prevalent during the rainy season, there are enough misty days during the dry season to maintain a relatively high constant humid condition.

5. Elfin Woodland (*Quercus-Clusia-Podacarpus* Association); Plate 9.

This formation is the highest in the Montane sequence and is limited to the upper ridges and crater rims and walls of the three principal volcanoes. The forest begins approximately at 4,800 feet on Volcáns San Martín Tuxtla and Santa Marta and at 3,400 feet on Volcán San Martín Pajapan. However, on ridges that are very steep and frequently exposed to strong winds (particularly on Volcán San Martín Pajapan and Cerro Tuxtla), elements of this formation occur at much lower elevations (as low as 2,700 feet). The numerous ravines within this formation contain elements of the Montane Thicket and/or Montane Rain Forest.

Ground vegetation is very luxuriant and consists of a thick mat of mosses and lichens that support profuse numbers of orchids and bromeliads. Where the canopy is relatively open and light penetration is good, grasses, principally *Aulonemia* sp. and *Isachne arundinacea,* the sedge *Rynchospora tuerckheimii,* and numerous small bushes and shrubs such as *Miconia glaberrima, Centropogon affine,* and *Solanum* spp. are common. The fern *Gleichenia palmata* and the cactus *Agave* sp. are locally common, especially on open, exposed ridges.

There is but one tree stratum and this consists of a gnarled, interlaced, many branched, and almost impenetrable growth of small trees ranging between 8 and 20 feet in height and con-

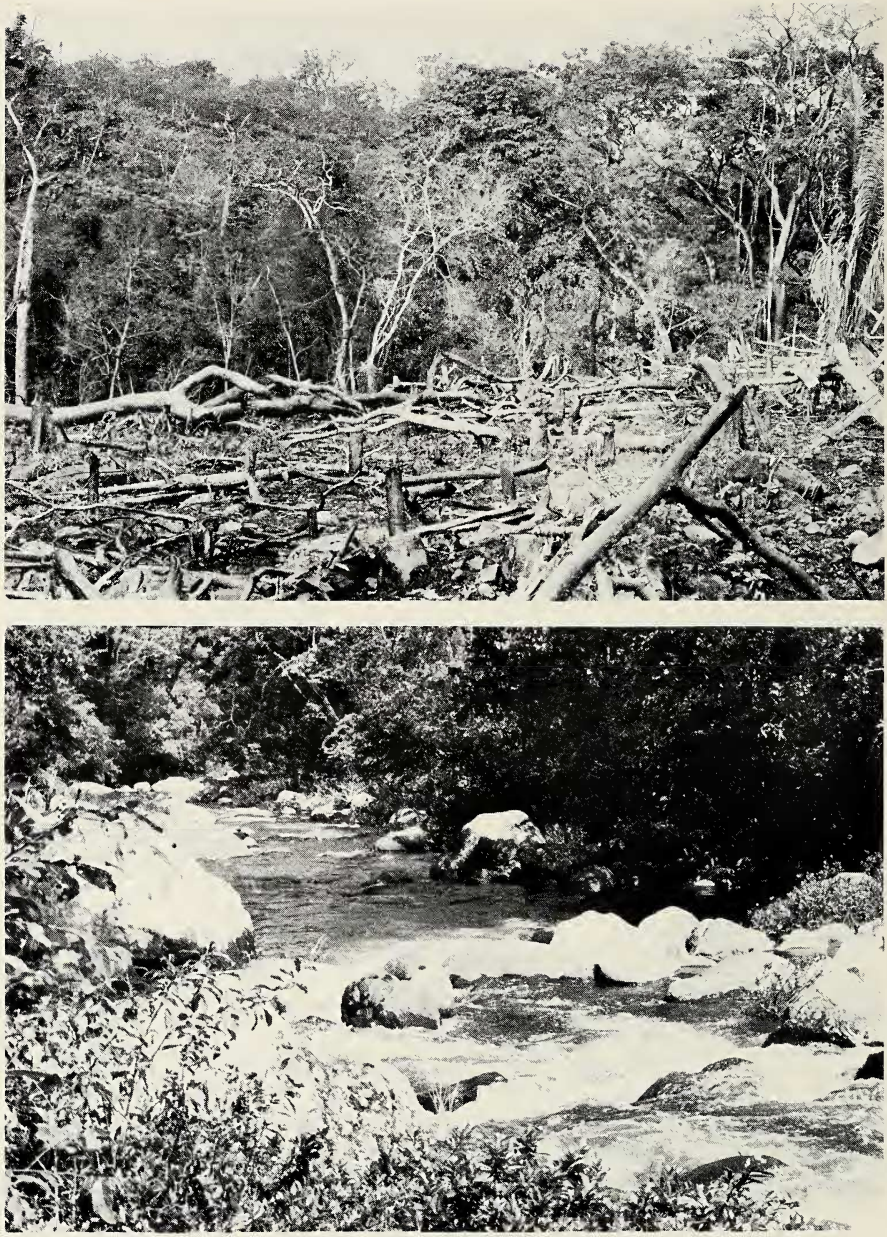

PLATE 10
Semi-Evergreen Seasonal Forest. TOP, forest near Barrosa. Area in foreground was cut and burned for corn cultivation. June 1962, 500 feet. Photograph from Andrle (1964) and used with the author's permission. BOTTOM, forest in ravine on Volcán Santa Marta near Ocotal Chico. July 1965, 1,700 feet.

sisting of *Quercus ghiesbrechtii, Clusia salvinii, Podacorpus oleifolius, Albizia* sp., *Phoebe psychotrioides, Ardisia* sp. (?), *Weinmannia pinnata, Gaultheria* sp., *Myrica cerifera, Solanum* sp., *Ceiba pentandra,* and *Gymnanthes actinostemoides.* Andrle (1964) recorded the following additional species: *Senecio* sp., *Hoffmania lenticillata, Viburnum acutifolium, Ilex nitida, Oreopanax xalapense,* and *Clethra suaveolens.*

Practically every branch, limb, and trunk is profusely festooned with mosses, principally *Pterobryum densum* and *Pilotrichella flexilis* (Andrle, 1964), ferns, lycopodiums, bromeliads, and orchids, principally *Elleanthus capitatus.* Many of the topmost branches of the tallest trees are dead. Not all species are evergreen; *Albizia* sp. (?) remains leafless during the dry season. Flowering and fruiting of all species are most common during the spring dry season.

Landslides resulting from mild earth tremors occasionally occur along the steep walls of the three primary craters (particularly on Volcán Santa Marta). These slides create openings in the forest and produce optimal conditions for primary succession. One of the most common angiosperms to appear shortly after a slide is *Schistocarpha* sp.

As stated previously, this formation and the Montane Thicket frequently are enveloped in mist, a fact that tends to make insect collecting very difficult.

SEASONAL FORMATIONS

6. Semi-Evergreen Seasonal Forest (Bursera-Inga Association); Plate 10.

This formation corresponds to the "Semi-Deciduous Forest" of Andrle (1964). Because of man's agricultural practices, the forest exists today only as remnants, principally on ridges and slopes in the southern part of the range where annual precipitation is usually less than 70 inches (primarily south of Cerro Cintepec), in the vicinity of Lago Catemaco, and in the numerous ravines within the Deciduous Woodland (including the *Pinus-Quercus* Associes) on the Santa Marta massif.

Ground vegetation is scanty although there is a dense understory of saplings and herbaceous plants. Common species include *Piper* spp., *Odontonema callistachyum, Acalypha diversifolia, Myriocarpa bifurca,* and *Heliconia latispatha.* The palm *Orbignya* sp. occurs sporadically throughout the formation.

Two tree strata are present. The lower stratum ranges be-

PLATE 11
Bursera-Sabal-Orbignya Forest near Tibernal, August 1962, 200 feet. Photograph from Andrle (1964) and used with the author's permission.

tween 15 and 30 feet in height and is composed principally of *Cecropia mexicana, Acalypha diversifolia* var. *carpinifolia,* and *Tabernaemontana citrifolia.* Along streams *Erythrina mexicana* is common.

The upper stratum ranges between 40 and 60 feet in height and consists primarily of *Bursera simaruba, Inga spuria, Inga leptoloba, Luehea speciosa, Myrcia splendens, Albizia idiopoda, Dendropanax arboreus, Ilex belizensis,* and *Roupala borealis.*

Trees usually branch low and the boles frequently are umbrella-shaped. Buttressing is uncommon. Trunks usually support numerous lianas and vines (such as *Anguria tabascensis*). Epiphytes are relatively uncommon.

During the dry season several of the dominants drop their leaves and remain leafless until the onset of the summer rains.

7. *Bursera-Sabal-Orbignya* Associes; Plate 11.

In the extreme southwest section of the range and at slightly lower elevations than the Semi-Evergreen Seasonal Forest is found a community that appears to be of subclimax rank. This forest is composed principally of *Bursera simaruba* and the palms *Sabal* sp. and *Orbignya* sp. Other trees include *Cecropia mexicana, Inga spuria, Cassia spectabilis,* and *Cassia occidentalis.* There is no definite canopy since the trees usually exist in dense, disjunct stands separated by extensive tracts of coarse grasses, sedges, and herbaceous plants of which the most common are *Paspalum* spp., *Sporobolus* spp., *Rynchospora* spp., *Dichromena ciliata, Asclepias woodsoniana, Melanthera angustifolia,* and *Stemodia durantifolia.* These open areas seem to be the result of, and, to be perpetuated by repeated burnings by the local Mexicans and intensive pasturing by livestock.

SEASONAL-SWAMP FORMATIONS

8. Savanna (*Curatella-Byrsonima* Association); Plate 12.

This formation, which seems to correlate well with the Orchard Savanna of Beard (1953), occupies a rather restricted area in the Sierra, principally south and southwest of the Santa Marta massif and at elevations below 450 feet. The formation intergrades with both the Semi-Evergreen Seasonal Forest and the Deciduous Woodland where contact exists.

PLATE 12
Savanna on Volcán Santa Marta near Guasuntlan. May 1962, 200 feet.
Photograph by R. F. Andrle.

Ground cover within the savanna is of variable density and consists principally of grasses, sedges, and woody plants of which the most common are *Paspalum* spp., *Panicum* sp., *Dichromena ciliata, Rynchospora* spp., *Asclepias woodsoniana, Stemodia durantifolia,* and *Melanthera angustifolia.*

The formation is rather open. Common trees include *Curatella americana, Byrsonima crassifolia, Apeiba tibourbou, Quercus oleoides,* and *Spondias mombin* (Andrle, 1964). These attain maximum heights of 10 to 20 feet.

Epiphytes are uncommon. Although leaves of most trees are shed annually (usually at the end of the dry season, May, or after the passage of fire), the trees never remain leafless for any extended length of time.

The reasons for the existence of this formation are debatable as they are for most other tropical savannas. Budowski (1959) states that experimental evidence indicates that all savannas would revert eventually to forest if fire is precluded from the area and if a seed source is near. However, there is not universal agreement on this matter. Beard (1953) states that "savanna may be characterized as the vegetation of the highly mature soils of senile land formations . . . which are subject to unfavorable drainage conditions in the form of intermittent perched water tables, with alternating severe periods of water logging and dessication." Furthermore, he continues and states that although the savanna may be swept by regular fires and the vegetation be adapted as to be fire resistant, the vegetation is not dependent upon fire for its maintenance but is an edaphic climax.

The Beard hypothesis seems to be the more reasonable explanation for the existence of the savanna in the Sierra. First, the formation occurs in one of the most ancient geological areas in the range (the Santa Marta massif) and the grey to black clay soils probably indicate severe leaching has occurred (Friedlaender, 1923). Second, the land is of low relief and there are numerous outcroppings of bedrock, two factors that probably make drainage relatively inefficient. Third, the annual precipitation, as recorded at Guasuntlan, averages approximately 67 inches and there are at least five months of the year that receive less than four inches of rainfall (Andrle, 1964). Fourth, the area has very few human inhabitants (and probably has had very few in the past) and so man-caused fires are relatively uncommon.

PLATE 13
Deciduous Woodland on Volcán Santa Marta near Soteapan. June 1965, 1,700 feet.